MACHAERIDIANS FROM THE UPPER WENLOCK (SILURIAN) OF GOTLAND

by ANETTE E. S. HÖGSTRÖM

ABSTRACT. Machaeridians, enigmatic animals widespread in Palaeozoic strata, have been known for approximately 130 years but nevertheless remain a little studied and problematical group. Two species of machaeridians (*Lepidocoleus* sp. A and *Turrilepas* sp. A) from the Upper Wenlock of Gotland are described. They occur commonly at Möllbos, with a preservation that allows tentative reconstruction of their morphology and interpretation of the function of the scleritome. The material corroborates the existence of outer sclerites in the Lepidocoleidae and exhibits variability of outer and inner sclerite shape along the body in the Turrilepadidae.

MACHAERIDIANS are a group of problematical, worm-like animals of Palaeozoic age, with an outer skeleton consisting of calcitic sclerites arranged in two or four longitudinal series. The systematics of the group are largely based on T. H. Withers' (1926) monograph of a collection housed mainly in The Natural History Museum. Their phylogeny and affinities are still largely unstudied, but following especially Bengtson (1978), they are considered to be 'metamerically arranged' protostomians with possible close affinities to molluscs, annelids, or arthropods. Recently there has been a renewed interest in the machaeridians, and some important works have been published (Bengtson 1977, 1978; Jell 1979; Dzik 1986; Adrain *et al.* 1991; Adrain 1992).

The Silurian strata of Gotland are comparatively rich in machaeridian skeletal remains, and like many other fossils from this island are often exquisitely preserved. Gotland machaeridians have not been formally described but have been reported quite frequently in the literature (e.g. Aurivillius 1892; Moberg 1914; Hede 1917; Bengtson 1979). A thorough study is thus long overdue. This paper will deal with material from the locality Möllbos 1 in the Upper Wenlock Halla Beds. The purpose is to describe the two most common machaeridians and to introduce some ideas on the appearance and function of their scleritomes. The use of open nomenclature is motivated mainly by the mode of preservation of machaeridians at Möllbos. There is a large amount of isolated sclerites and a number of, often deformed, assemblages. None of these, however, is well suited for the designation of a species, although many previously described taxa have been based on less perfect material.

GEOLOGY

The material is derived from the locality Möllbos 1, representing the middle unit of the Halla Beds, Halla b (Laufeld 1974*a*). The Halla Beds correspond to the Upper Wenlock and consist of thin-bedded strata deposited in shallow water. According to Laufeld (1974*b*), their thickness on Gotland is around 15 m in the north-east (the Hörsne-Gothemshammar area), where three lithostratigraphical units crop out. The lowest unit, a, is 3·5–4 m thick with almost white, oolitic limestone enclosing small bioherms. The middle unit, b, consists of 6–6·5 m of bituminous and argillaceous limestone, also with bioherms. Unit c is the highest and consists of 5 m of argillaceous limestone intercalated with thin laminae of marlstone. This unit is terminated by a discontinuity surface. Towards the south-west the beds decrease in thickness and are replaced by the Mulde Beds of approximately equivalent age.

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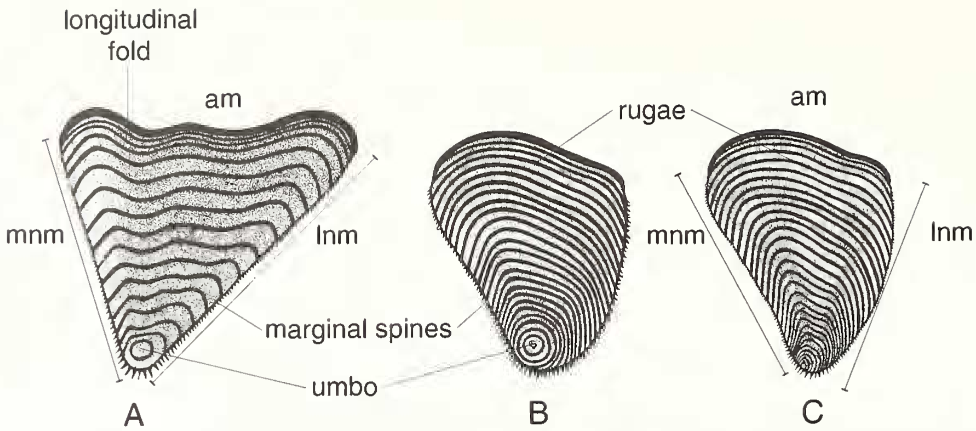


TEXT-FIG. 1. Schematic illustrations of the sclerites belonging to *Turrilepas* sp. A. The thick line denotes the accreting margin. A, inner right sclerite with modified apical region. B, modified outer right sclerite. C, unmodified outer right sclerite. *am*, accreting margin; *lnm*, lateral non-accreting margin; *mnm*, medial non-accreting margin. Not to scale.

Möllbos 1 is a low and easily accessible rivulet section, with a lateral extent of around 140 m. The section is located immediately north-west of the dam at the pond. Möllbos 2 is exposed along the same stretch, approximately 150–175 m from the dam.

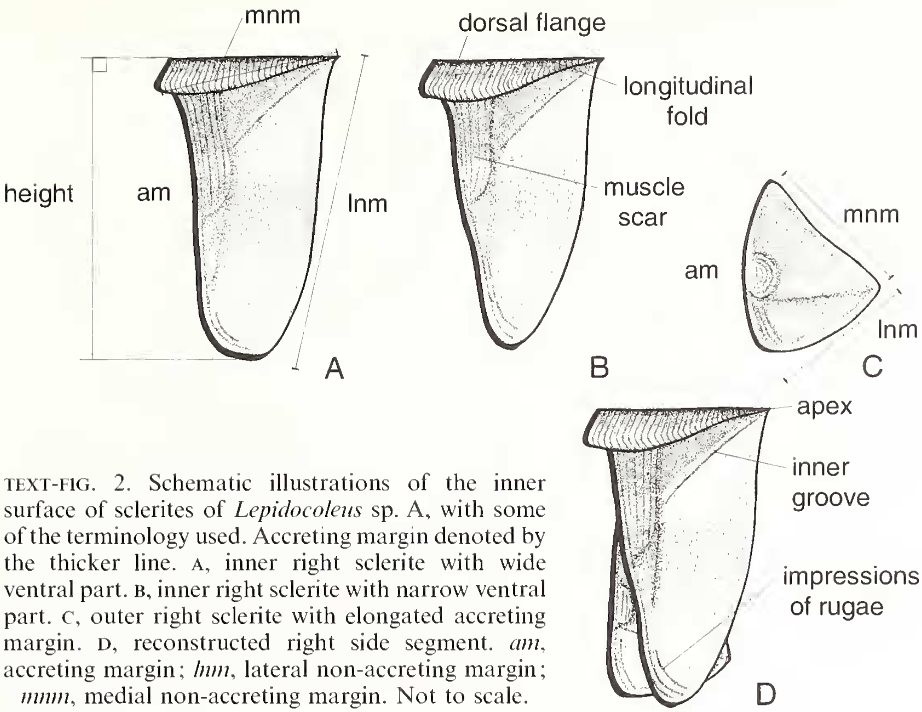
The rocks at Möllbos 1 consist of argillaceous bedded limestone intercalated with thin marly layers; at Möllbos 2 there is a bioherm. Between the bioherm and the bedded deposits there is an area consisting of debris from the bioherm (Hede 1960). This locality has been interpreted as a reef-lagoonal environment (e.g. by Hede 1960). Hede also considered fossils to be scarce at the locality, but subsequent studies on silicified material have shown that the limestone is richly fossiliferous (e.g. Liljedahl 1984, 1985, 1986).

MATERIAL

The material consists of specimens obtained from loose blocks of limestone collected at Möllbos 1, in the summers of 1991 and 1992, and material collected by J. E. Hede in the 1940s, housed in the Department of Historical Geology and Palaeontology, University of Lund. The specimen numbers consist of a prefix followed by a serial number, where PMU stands for the Palaeontological Museum Uppsala University, and LO for the Palaeontological Institute of the University of Lund. Before photography the specimens were lightly dusted with ammonium chloride sublimate.

TERMINOLOGY

The terminology has been adapted from Adrain *et al.* (1991) and Adrain (1992), with a few exceptions. Inner sclerites of the order Turrilepadomorpha are folded at an angle of usually 90°; the fold extends all the way from the accreting margin to the apex. Adrain *et al.* (1991) used the term *longitudinal angle* when referring both to the fold and to the angle of the fold. These will instead be referred to as *longitudinal fold* and *angle of the longitudinal fold*, respectively (see Text-fig. 1). Adrain *et al.* (1991) also used the term *longitudinal angle* when considering outer sclerites in the diagnosis of, e.g. *Turrilepas wrightiana* (de Koninck, 1857); 'length of accreting margin of outer sclerites subequal to length of longitudinal angle of outer sclerites' (Adrain *et al.* 1991, p. 644). Here the usage of *longitudinal fold* is restricted to the inner sclerites. In lepidocoleids the size is given as height of the sclerite and length of the longitudinal fold (Text-fig. 2). The height is measured from the most



TEXT-FIG. 2. Schematic illustrations of the inner surface of sclerites of *Lepidocoleus* sp. A, with some of the terminology used. Accreting margin denoted by the thicker line. A, inner right sclerite with wide ventral part. B, inner right sclerite with narrow ventral part. C, outer right sclerite with elongated accreting margin. D, reconstructed right side segment. *am*, accreting margin; *lnm*, lateral non-accreting margin; *mnm*, medial non-accreting margin. Not to scale.

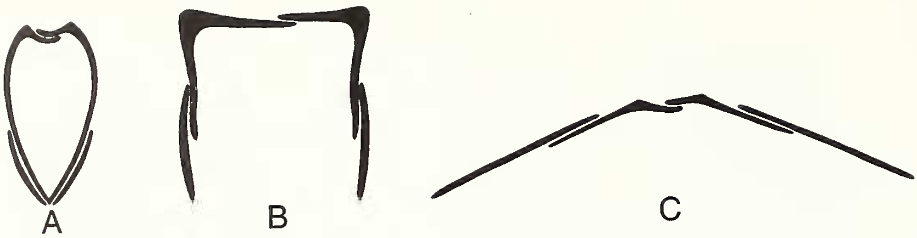
ventral point to the longitudinal fold, rather than as the length of the accreting margin, since the latter has a somewhat complex morphology in lepidocoleids and is difficult to measure correctly and efficiently. It should also be noted that the term *segment* is used descriptively, without implicit assumptions of the type of metamerism involved.

GENERAL MORPHOLOGY OF SCLERITOMES

Machaeridian scleritomes are of two main kinds, represented by the orders Lepidocoleomorpha and Turrilepadomorpha. The major differences between them lie in the number and arrangement of sclerites and in the presence or absence of a functional dorsal hinge. The universally present muscle scars are currently the best known indicators of soft part anatomy. Jell (1979) reported structures interpreted as head palps in *Plumulites richorum* (Jell, 1979) from early Devonian strata in Australia, but Dzik (1986) presented a more plausible interpretation of the structure, suggesting that the anterior end of the animal had been tucked under the rest of the body with the 'palps' then representing apical parts of inner sclerites.

Lepidocoleomorpha

The lepidocoleomorphs have often been called biseriate machaeridians (e.g. Adrain 1992; in the diagnosis of the order Lepidocoleomorpha) since they have been assumed to possess only two series of sclerites. Dzik (1986), however, reported traces of outer sclerites in *Lepidocoleus ketleyanus* (Reed, 1901), and the present material from Gotland shows this feature in at least part of the scleritome. It is not clear, however, how common it is among lepidocoleids. The inner sclerites of a lepidocoleid are dorso-ventrally elongated, with a distinct dorsal flange constituting the hinge (see Text-fig. 3A for cross section of a scleritome). Adrain (1992) described a special kind of hinge structure in some



TEXT-FIG. 3. Schematic cross sections of the three types of machaeridians discussed in the text. A, species of Lepidocoleidae with outer sclerites, e.g. *Lepidocoleus* sp. A. B, Turrilepadidae. C, Plumulitidae. Not to scale.

lepidocoleids, which he called *tongue-and-groove hinge* (see especially Adrain 1992, fig. 5). This hinge was considered to be a general feature of lepidocoleids, but, as the material from Möllbos shows, there are species without such a structure (they have only relatively large overlapping dorsal flanges). Lepidocoleids are currently the only machaeridians known with a functional hinge. Lepidocoleid scleritomes can be quite long; e.g., *L. ketleyanus* has a minimum of 60 segments. At present there are several types of lepidocoleids classified together, but the resolution of the taxonomic problems lies beyond the scope of this paper.

Turrilepadomorpha

This order includes the quadriseriate machaeridians as traditionally understood. The two families Turrilepadidae and Plumulitidae are separated on the basis of different sclerite arrangement (Jell 1979). Both families have inner sclerites with a distinct longitudinal fold; in at least the turrilepadids there are two morphologies of the inner sclerites. The medial part of one side (usually the left) is larger than the corresponding medial part on the other (usually the right) side (Adrain *et al.* 1991). Outer sclerites, however, are nearly perfect mirror images of each other and are essentially flat. There is a distinct anterior region in both families, with the outer sclerites of the first two segments absent (Adrain 1992). Some have modified outer sclerites in the following two or three segments; until now this feature has only been described in plumulitids (e.g. Barrande 1872; Jell 1979), but turrilepadids from Möllbos exhibit the same kind of modification of outer sclerites (Pl. 1, fig. 8). Turrilepadids have a more-or-less square body cross section resulting from the 90° angle of the longitudinal fold (Text-fig. 3B), except in the anterior region where the fold is only slightly expressed, resulting in a flatter appearance. By segment 5 or 6 the angle of the longitudinal fold is fully expressed (Adrain *et al.* 1991).

In plumulitids the angle of the longitudinal fold is less acute than in turrilepadids, approximately 150° or larger, resulting in a broad ventral body surface and a triangular rather than square body cross section (Text-fig. 3C). Jell (1979, fig. 3c) revised Withers' (1926) erroneous cross section of a plumulitid, but Jell probably separated the sclerites excessively. The sclerites had to overlap if they were to form a total cover of the dorsal side. Plumulitid outer sclerites are considerably larger than their inner ones; in turrilepadids the inner sclerites are somewhat larger.

Preservation

The preservation of machaeridians at Möllbos is commonly very good, but they are usually not silicified as, for example, the bivalves are. Lepidocoleids make up around 80 per cent. of the machaeridians at Möllbos. Most machaeridians at Möllbos are preserved as isolated sclerites, but the locality is also rich in assemblages, especially of lepidocoleids. The higher number of preserved lepidocoleid assemblages is presumably due to their dominance in the fauna and to their ability to close their scleritome fully. There is a difference in the preservation of isolated sclerites on rock surfaces: lepidocoleids almost exclusively expose the inner surface, whereas turrilepadids expose the outer one. This appears to be due to a very thin innermost layer on lepidocoleid sclerites, along which the rock is easily parted. The nature of this layer is currently unknown. When the layer is flaked off, the granulated inner surface appears more distinct than in sclerites with the layer preserved. Turrilepadids from this locality do not appear to possess any such layer, and their granulated inner surfaces tend to adhere to the rock.

SYSTEMATIC PALAEONTOLOGY

Class MACHAERIDIA Withers, 1926
Order LEPIDOCOLEOMORPHA Schallreuter, 1985
Family LEPIDOCOLEIDAE Clarke, 1896

Genus LEPIDOCOLEUS Faber, 1886

Lepidocoleus sp. A

Text-figure 4A–I

Material. Illustrated specimens: LO 7368t, LO 7369t, LO 7365t, LO 7366t, LO 7367t, PMU G1017, PMU G1018, PMU G1019; additional material consisting of seven more-or-less complete assemblages, and approximately 126 isolated, complete or fragmented sclerites.

Description. Inner sclerites usually large and robust, dorsoventrally elongated; all sclerites with ventral part slightly narrower than dorsal one, but some are very much narrower, down to one-third of the length of the longitudinal fold (Text-fig. 4C). Most sclerites have a height of around 5 mm and a length of the longitudinal fold of approximately 2·5–3 mm, but large specimens with a height of 7·5–8 mm are known. Inner surface granulated, with a large, elongated muscle scar, usually around 40–60 per cent. of the height of the sclerite, situated close to the dorsal flange and to the accreting margin of the sclerites (Text-fig. 4A, F). Impressions of the rugae are seen on the inner surfaces on most sclerites; they are often distinct, especially in the muscle scar. Inner groove also distinct, running between apex and muscle scar (as in Text-fig. 4F). Outer surface usually adheres to rock; the rugae are very fine and almost indiscernible, density approximately 5–7 per mm (see Text-fig. 5 for reconstruction of the pattern of rugae). Density of rugae is slightly higher close to the accreting margin and especially in the dorso-ventral direction. Small apical spines are present, but no traces of marginal spines. Dorsal flanges largest anteriorly, but without any tongue and groove-hinge structures as described by Adrain (1992, fig. 5).

Outer sclerites have a roughly triangular outline and are essentially flat (although the largest ones are slightly curved in cross section, in order to fit closely alongside the inner sclerites). Accreting margin very often elongated (Text-fig. 4G), around 3·5–4·5 mm long; lateral non-accreting margin around 4 mm, and medial non-accreting margin 4–5 mm. Inner surface similar to that of inner sclerites except that the muscle scar is smaller and more rounded (Text-fig. 4G–I). Inner groove distinct and running between the ventral part of the muscle scar and the apex (Text-fig. 4G–I). Outer surface not well exposed in the material and therefore the density of rugae can only be estimated approximately, around 5 per mm, very fine as on the inner sclerites (see Text-fig. 5 for reconstruction). Possibly the rugae are also more closely spaced near the accreting margin in the outer sclerites. Outer sclerites show no traces of any apical or marginal spines. Differences in general outline between the outer sclerites may depend on their placement within the scleritome (Text-fig. 4G–I). Total number of isolated outer sclerites recovered from the locality is lower than the number of isolated inner ones, approximately 47 per cent. of 126 sclerites (material too badly preserved for identification has been excluded).

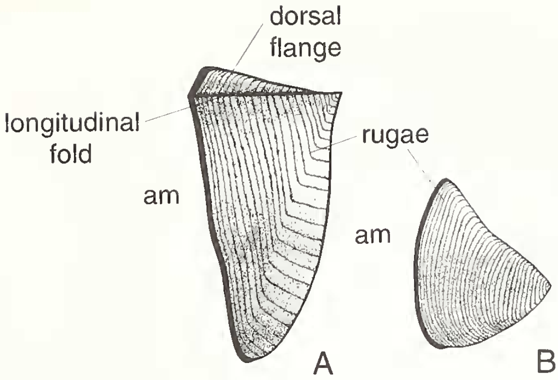
Specimen LO 7368t (Text-fig. 4C–D) partly exposes a cross section, presumably from somewhere along the undifferentiated mid-part of a scleritome. The specimen may be divided roughly into two parts: a posterior part projecting into the rock, only partially exposed, and an anterior part that has been compressed in longitudinal direction so that the segments lie partly on top of one another; hence the estimate of number of segments is slightly uncertain. Approximately 11 or 12 segments are visible in the anterior part but some are badly preserved and exposed. The first seven segments only have left sclerites preserved, exposing their inner surfaces. Best exposed here is sclerite 6, which is a partially complete inner sclerite exhibiting a prominent muscle scar and a narrow ventral part (right arrow, Text-fig. 4C). The following segments, 8–12, have both left and right sides poorly preserved. The most posterior sclerite is the impression of an outer right one (left arrow, Text-fig. 4C) with the muscle scar exposed as a rounded elevation on the surface. A cross section of the assemblage is

TEXT-FIG. 4. *Lepidocoleus* sp. A; Möllbos 1, Halla Beds, Gotland, Upper Wenlock, Silurian, A, LO 7365t; detail of the assemblage; ×4. B, LO 7369t; general view, note outer sclerites (arrows); ×4. C–D, LO 7368t. C, general view of the assemblage; ×5. D, cross sectional view; ×5. E, LO 7366t; inner surface of one right side segment; ×6·5. F, LO 7367t; inner surface of an inner right sclerite; ×5. G, PMU G1019; inner surface of an outer left sclerite; ×8. H, PMU G1017; inner surface of an outer right sclerite; ×6·5. I, PMU G1018; inner surface of an outer right sclerite; note differences in outline from PMU G1019 and PMU G1017; ×6·5.

figured in Text-figure 4D. The right side has slipped dorsally, thus the width of the cross section is narrower than the width of the original scleritome.

Specimen LO 7369t (Text-fig. 4B) derives also from the undifferentiated part of a scleritome. The estimated number of preserved segments is nine or ten. In the anterior portion of the assemblage only displaced and fragmented right sclerites, exposing inner surfaces, are preserved. There are prominent muscle scars exposed in three of them. At least one of the sclerites is an outer one with a more rounded muscle scar, an elongated accreting margin and inner groove (Text-fig. 4B, left arrow). The left side is preserved in the posterior part of the assemblage, where the best exposure of outer surfaces is found. The first segment on the posterior part

TEXT-FIG. 5. Reconstruction of the outer surfaces of sclerites of *Lepidocoleus* sp. A. Thick line denotes the accreting margin. A, inner left sclerite. B, outer left sclerite. *am*, accreting margin. Not to scale.



exposes a complete impression of a large outer sclerite with elongated accreting margin, muscle scar and an inner groove (Text-fig. 4B, central arrow). Beneath this impression the outer surface of an inner sclerite is distinguishable. The following four segments are partly exposed and the spatial relationship between them appears to have been subject to relatively little distortion. Traces of probable outer sclerites are detectable between the inner sclerites (Text-fig. 4B, right arrows).

LO 7365t (Text-fig. 4A) is the largest specimen. Distortion of the assemblage has been quite considerable, producing a splayed-out configuration of the sclerites. The figured part of the assemblage exhibits mostly sclerites from the right side. All but two are nearly completely buried in sediment. These two visible sclerites (Text-fig. 4A, arrows) are one outer and one inner sclerite. The outer sclerite (left arrow) has a distinct muscle scar and an elongated accreting margin; the apical region, however, is not exposed. The inner one (right arrow), situated about two segments posterior to the outer sclerite, is complete except for the lost dorsal flange; a distinct muscle scar and inner groove are clearly exposed. Both sclerites have remains of the thin innermost layer preserved along their non-accreting margins. Posterior to the described inner sclerite, there are two impressions of large, outer left sclerites which have been twisted considerably out of place, so as to attain a reverse orientation in relation to the right-hand sclerites. They expose prominent, rounded muscle scars, inner grooves and elongated accreting margins. Most of the surfaces are covered with the thin innermost layer. The most posterior part (unfigured) of the assemblage has been severely affected by distortion and consists of various fragmented inner and outer sclerites.

Specimen LO 7366t (Text-fig. 4E) is a small portion of an assemblage. The sclerites of the right side of five segments are preserved. They are compacted on top of each other, resulting in a minimum exposure of all but one segment. The dorsal flanges of all the inner sclerites are broken off. Best exposed is the inner surface of the most posterior segment (Text-fig. 4E). The inner sclerite is broken immediately dorsal and ventral of the muscle scar, thus exposing the outer sclerite beneath it. The inner sclerite shows the muscle scar and the inner groove. Remains of the thin innermost layer are preserved along the lateral non-accreting margin of the sclerite. A set of wrinkles is visible adjacent to the lateral non-accreting margin, oriented roughly in an apical direction. The function of these wrinkles is at present unknown. The outer sclerite is not completely exposed; the muscle scar and dorsalmost parts are concealed beneath the inner sclerite. Clearly visible, though, is the inner groove and quite large portions of the thin innermost layer preserved along the margins. As with the other described assemblages, the outer sclerites are large. The spatial relationship between the sclerites in the specimen is not entirely undisturbed. The specimen has been compacted, and the sclerites seem to have been slightly twisted in relation to each other, thus hiding the muscle scar of the outer sclerite beneath the inner sclerite.

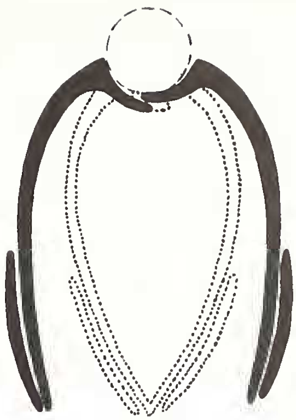
Specimen LO 7367t (Text-fig. 4F) is a separate inner sclerite, and specimens PMU G1017, PMU G1018, and PMU G1019 (Text-fig. 4G–I) are separate outer sclerites.

Reconstruction. The reconstruction proposed here is based on the present material from Möllbos and comparisons with, especially, *L. ketleyanus*. Described specimens LO 7368t, LO 7369t, LO 7365t, and LO 7366t were particularly useful.

Lepidocoleus sp. A has a total length of at least 20–25 segments, and it is only the second known lepidocoleid with outer sclerites. Dzik (1986) reported small outer sclerites in *L. ketleyanus*, but it is not clear whether he considered them to exist throughout the entire scleritome. Neither of the two above species has the anterior end preserved; the posterior end, however, is partly preserved in the large specimen of *L. ketleyanus* from the Much Wenlock Limestone at Dudley, Worcestershire, housed at the Lapworth Museum, Birmingham University (Holcroft Collection, no. 62, figured previously by Withers 1933, pl. 4:4; and Bengtson 1977, fig. 3). In *Lepidocoleus* sp. A the placement of the outer sclerites is uncertain, but comparing the total number of outer and inner sclerites may give some idea of the scleritome organization. The lower number of outer sclerites may be interpreted as a condition where part of the scleritome was composed only of inner sclerites; which part, however, it is not possible to say. There may be a slight taphonomic bias in the count of sclerite types. Outer sclerites were not attached to the soft parts as firmly as inner ones; the muscle was smaller, and the area in contact with soft tissues was also considerably smaller for outer sclerites. Thus the probability for post-mortem dispersal and fragmentation is likely to be somewhat higher for the outer sclerites. This possible difference in preservation may thus affect the number of sclerite types and hence also the reconstruction. Based on comparisons with other machaeridians, it is very probable that the anterior end in *Lepidocoleus* sp. A had modified sclerites. Distinct anterior ends are known from e.g. *Turrilepas wrightiana* (see Adrain *et al.* 1991), *Plumulites richorum* Jell, 1979 and *Lepidocoleus sarlei* Clarke, 1896, i.e. from all three families. The number of segments constituting this anterior end may differ somewhat, and it is not possible to draw any conclusions concerning the number in *Lepidocoleus* sp. A based on the available information. The undifferentiated mid-part section of the scleritome in *Lepidocoleus* sp. A includes *c.* 15–20 segments (a tentative estimate). At least in part of this section, the segments are composed of both inner and outer sclerites. Specimens LO 7368t, LO 7369t, LO 7365t, and LO 7366t have inner and outer sclerites closely associated (Text-fig. 4A–E). The inner ones have a distinctly narrower ventral part (Text-fig. 4A, C), down to one-third of the length of the longitudinal fold. Outer sclerites are large and have an elongated accreting margin. The outer sclerites overlap the inner ones (see especially specimen LO 7366t and LO 7369t where the overlap is clearly exposed, although in LO 7369t only an impression of the outer sclerite is preserved; Text-fig. 4B, E). One segment is reconstructed in Text-figure 2D. The most probable reason for the inner sclerites of *Lepidocoleus* sp. A being narrower in the ventral part is to allow the insertion of the muscle adhering to the outer sclerite. This feature is also of potential value in identifying species where outer sclerites probably were present but are not preserved. The partly preserved posterior end in *L. ketleyanus* shows a continuous decrease in size over several segments (Withers 1933, pl. 4:4; and Bengtson 1977, fig. 3). The posterior structure of *Lepidocoleus* sp. A is probably quite similar. The very last posterior segment is not known. In *L. sarlei* and possibly also in *Lepidocoleus jamesi* (Hall and Whitfield), the pattern of rugae is modified on the minute posteriormost sclerites. The dorsal hinge in *Lepidocoleus* sp. A did not articulate by means of a tongue-and-groove hinge; there are only simple overlapping dorsal flanges. The material does not reveal whether the right side overlaps the left or vice versa. The sclerites do not appear to be enantiomorphic as are those of other lepidocoleids (Adrain 1992). Both sides in *Lepidocoleus* sp. A developed the largest part of the dorsal flange anteriorly, and the continuous hinge appears to be a result of the posterior imbrication of the sclerites. Width of the dorsal depression constituting the hinge is approximately 1–1·5 mm. The resulting cross section of *Lepidocoleus* sp. A is that of a high and narrow scleritome, similar to the cross section of *L. ketleyanus*.

Functional morphology. The cross section of *Lepidocoleus* sp. A resembles that of a bivalve except for the outer sclerites and the hinge structure. Wolburg (1938) reconstructed *Aulakolepos gleidorfense* (Wolburg, 1938) with a ligament positioned in the dorsal depression constituting the hinge, with the assumption that the scleritome functioned more or less like a segmented bivalve. There is no evidence, however, to support the presence of a ligament in the Lepidocoleomorpha. Closing of the lepidocoleid scleritome was presumably accomplished by contraction of the large muscles adhering to the inner sclerites. The opening of the scleritome could not have been accomplished directly by muscle power, as there is no evidence of antagonistic muscles to the ones closing the scleritome. The most probable alternative is the use of hydrostatic pressure. In elongated animals, such as lepidocoleids, a feasible option is the creation of a pressure wave propagating

TEXT-FIG. 6. Schematic cross section of *Lepidocoleus* sp. A illustrating the difference between the closed and the open scleritome. Not to scale.



through the body. Owing to the posterior overlap of the sclerites, the anterior end would be the first part to open.

The overlap of the dorsal flanges would somewhat complicate the process of opening. In bivalves, for example, there is no overlap; the shell halves meet in the hinge. In lepidocoleids the dorsal flanges would have to remain parallel while moving apart in order to achieve a smooth rotation. The movement should follow the outline of an imaginary cylinder placed in the dorsal depression constituting the hinge (Text-fig. 6). A relatively small amount of dorsal rotation (15–20°) will correspond to a ventral opening of approximately 2·5 times wider than the width of the dorsal depression (Text-fig. 6).

The amount of separation of the dorsal flanges is limited by the flexibility of the soft parts and by the apical regions abutting against each other after a certain amount of rotation. The latter may be of importance, especially in lepidocoleids which have a very narrow dorsal depression.

Clark (1964, pp. 31–35) described the general processes for inflation of the body in a simple animal with only circular muscles in the body wall. This, however, is probably not the optimal body organization for lepidocoleids, as the control over smaller parts of the body is low and the result most likely would be a fairly inefficient opening process. Segmentation would give lepidocoleids more possibilities than mere contractions of either end of the body, as it would be possible to employ a small part of the body at a time (Fretter and Graham 1976). This is a controlled and energetically efficient way of opening the scleritome. A drawback is that the maximum pressure in each segment is likely to be low because of the small volume of each segment (Fretter and Graham 1976).

The actual body plan of lepidocoleids (and other machaeridians) is not well understood. The sclerite segments and the muscle arrangement indicates more than a superficial division. Complete transverse coelomic partitions may not be necessary, however, for the opening of the scleritome to function sufficiently well.

Order TURRILEPADOMORPHA Pilsbry, 1916
Family TURRILEPADIDAE Clarke, 1896
Genus TURRILEPAS Woodward, 1865
Turrilepas sp. A

Plate 1, figures 1–8

Material. Illustrated specimens: LO 7371t, LO 7370t, PMU G1020; additional material consisting of three more or less complete assemblages, and approximately 30 isolated, complete or fragmented sclerites.

Description. Large and robust sclerites, inner ones with a length along the longitudinal fold of *c.* 4–5 mm; accreting margin 5–7 mm. Density of rugae approximately 4–5 per mm, total number 18–24. Spacing of the rugae is fairly even over the sclerite surface; there is a tendency for rugae close to the accreting margin to be closer set. The apex (since modified) is also somewhat different from rest. The rugae tend to be quite straight (Pl. 1, figs 2, 5) compared with the more wavy pattern of *T. wrightiana.* Marginal spines number approximately two or three between each ruga; spines larger in apical region than close to the accreting margin (Pl. 1, figs 2, 5). No apical spine on the inner sclerites; instead the umbo is displaced away from the apex producing concentric rugae in the apical region (Pl. 1, figs 3, 5). The rugae are expressed most distinctly when they transect the longitudinal fold and become less distinct on the medial and lateral parts, although the medial part is smoother overall than the lateral one. This apparently corresponds to the pattern of rugae in *T. wrightiana* and *Turrilepas modzalevskae* (Adrain *et al.* 1991). Inflections I_1–I_5 are all present but are not as well expressed as in *T. wrightiana* and *T. modzalevskae.* I_3 is almost indistinguishable, but I_2 and I_4 are also shallower than in *T. wrightiana* and *T. modzalevskae*, resulting in the straight pattern of rugae. Inner surfaces are rarely exposed; where visible the only observed structure is the distinct granulation of the surface.

Outer sclerites occur in two morphologies (Pl. 1, figs 4, 8). The less common form (specimen PMU G1020, Pl. 1, fig. 8, only recovered sclerite of this type) has the umbo placed away from the apex producing distinct concentric rugae in the apical part and also a quite pronounced roundness of the apical region. This is similar to the modified outer sclerites of *Plumulites richorum*, also exhibiting a more rounded shape (Jell 1979). Outer sclerites in *Turrilepas* sp. A usually have a slightly pointed apex but no real apical spine. These sclerites are relatively similar to the outer ones in *T. modzalevskae.* Both *Turrilepas* sp. A and *T. modzalevskae* have shorter accreting margins than *T. wrightiana*, resulting in a more antero-posterior elongated appearance. The size of the modified and unmodified sclerites in *Turrilepas* sp. A is similar; length of medial non-accreting margin 5–7 mm; accreting margin 4–6 mm. The density and total number of rugae differ between the two; modified sclerites have a density of approximately 4–5 per mm (the apex is different because of the modification), total number 20–25; unmodified ones have a density around 5–7 per mm (rugae tend to be closer spaced near the accreting margin), total number 35–45. The density of rugae on the unmodified outer sclerites in *Turrilepas* sp. A is higher than in both *T. wrightiana* and *T. modzalevskae.* Marginal spines approximately four or five between each ruga, larger in the apical region than close to the accreting margin. The rugae on the unmodified sclerites are more distinctly pronounced on the lateral part than on the medial one (Pl. 1, fig. 4). The boundary between the lateral and medial parts appears to correspond to the inner groove of the inner surface. In *T. wrightiana* and *T. modzalevskae* a similar condition seems to exist, although the boundary between the two parts may be situated closer to the lateral non-accreting margin. Inflections of *Turrilepas* sp. A: I_1–I_3 are all quite well defined, I_2 is more distinct than in *T. wrightiana* and seems to correspond to the boundary between lateral and medial parts on these sclerites (Pl. 1, fig. 7). The inner surface is almost never exposed; granulation is virtually the only observed structure on this surface.

Specimen LO 7371t (Pl. 1, figs 1–6) consists of a large portion of an assemblage with the right and left sides exposed, and the dorsal side completely covered by sediment. Mostly outer sclerites are visible, the posterior end is absent and the anterior end appears to have only a few segments missing. The left side of the assemblage (Pl. 1, fig. 1) is *c.* 30–31 mm long, with 21 segments exhibited (numbered from the first one visible). The first segment has only an inner sclerite preserved (Pl. 1, fig. 2). There is no apex preserved and the density of rugae is higher than in the subsequent inner sclerites. The angle of the longitudinal fold is *c.* 120–125° and the sclerite is also smaller than the others (approximately 5 mm, compared with 7–8 mm along the longitudfinal fold). The higher density of rugae, large angle of the longitudinal fold and the smaller size strongly indicates an anterior position in the scleritome. Segment 2 also lacks an outer sclerite and may be similar to segment 1, but this is difficult to judge from the small exposure. Segments 3–7 consist both of outer and inner sclerites, the inner sclerites having a lower density of rugae than the previous ones. Segment 8 has a large inner sclerite with a

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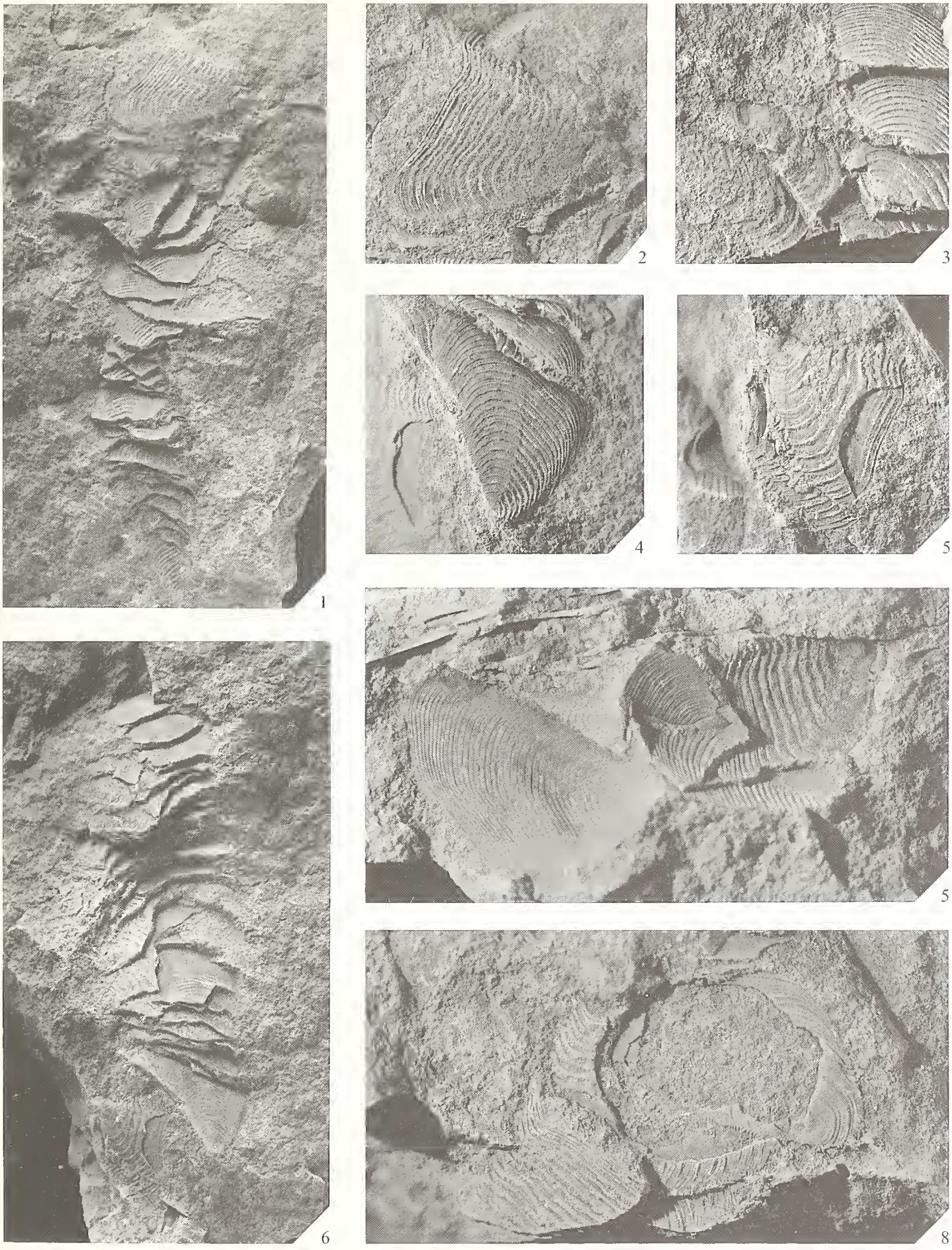
EXPLANATION OF PLATE 1

Figs 1–8. *Turrilepas* sp. A; Möllbos 1, Halla Beds, Gotland, Upper Wenlock, Silurian. 1–6, LO 7371t. 1, general view of the left side; ×3. 2, anteriormost inner left sclerite; ×5. 3, anteriorly placed inner right sclerite with displaced umbo; ×6·5. 4, posteriormost outer right sclerite; ×5. 5, posteriorly placed inner right sclerite with displaced umbo; ×5. 6, general view of the right side; ×3. 7, LO 7370t; impression of an inner right sclerite with displaced umbo and impression of an outer right sclerite; ×4. 8, PMU G1020; right side sclerites, especially outer sclerite with displaced umbo; ×4.



HÖGSTRÖM, *Turrilepas*

length along the longitudinal fold of at least 7 mm. The rugae are distinctly widely spaced and there are traces of a displaced umbo. Segments 9–20 have only traces or very small parts of the inner sclerites visible. Outer sclerites are present and do not differ much in appearance from each other. The last segment, no. 21, exposes the apical part of an outer sclerite; there is no apical spine present. Marginal spines of the lateral non-accreting margin appear larger and more widely spaced than the spines on the medial non-accreting margin. The right side of the assemblage (Pl. 1, fig. 6) has a length of 29–30 mm, with 21 segments exposed (numbered from the first one visible). Segments 1–2 consist of both inner and outer sclerites, the inner ones are hardly visible and the outer ones are partly broken. Segment 3 exhibits the apical portion of an inner sclerite with displaced umbo (Pl. 1, fig. 3). Widely spaced rugae are also present. The outer sclerite is partly broken, as are the two previous ones. Segments 4–18 are fragmentarily preserved, but still both the inner and outer sclerites are present in all segments and they are apparently uniform. Segment 19 exposes traces of an inner sclerite and a virtually complete outer one (Pl. 1, fig. 4). The apex on the outer sclerite is slightly worn; therefore no spines are preserved there. The marginal spines seem to be larger and fewer on the lateral margin and smaller, more numerous on the medial margin. The pattern of rugae clearly exposes two parts; a lateral part with prominent rugae and a medial part with less prominent rugae. Segment 20 has only the inner sclerite preserved, which has been twisted out of place. This sclerite clearly shows the displaced umbo but has a different pattern of rugae compared with other inner sclerites (Pl. 1, fig. 5). The density of rugae is lower, and the sclerite is also slightly smaller than the other inner ones. The inner sclerite of segment 21 is exposed beneath that of segment 20; it is not entirely complete and it does not correspond in appearance with segment 20 but rather with the rest of the inner sclerites. The outer sclerite of segment 21 has been lost. The left and right sides of the specimen do not match completely in appearance as would be expected in an undisturbed specimen. The left side appears to be derived from a more anterior position than the right. The most reasonable explanation is that the two sides have been displaced relative to each other and that the left side actually does represent a slightly more anterior portion of the scleritome.

Specimen LO 7370t (Pl. 1, fig. 7) is not as well preserved as specimen LO 7371t. It comprises a small part of an assemblage presumably from somewhere along the mid-part of a scleritome. The specimen is *c.* 10–11 mm long with *c.* 7–8 segments preserved. The largest part of the specimen exhibits the dorsal side. Most of the original sclerite material has been worn off, however, making the relationship between the sclerites hard to distinguish. The figured part of the specimen exposes a few right side sclerites preserved as impressions. They have been displaced so as to lie in the direction of a cross section of the assemblage. The most conspicuous of these impressions is the lateral part of an inner sclerite and a complete outer one. The inner sclerite exhibits a distinct displaced umbo and widely spaced rugae. The outer sclerite exhibits a well expressed I_2 and also a difference in distinctness of rugae. Between these two, fragments of additional outer sclerites are visible.

Specimen PMU G1020 (Pl. 1, fig. 8) is a small specimen consisting of *c.* eight right side segments, although most of them are hardly visible. The best exposed sclerite is an outer one with a displaced umbo. The other sclerites are inner ones, and one of them is markedly displaced (Pl. 1, fig. 8); its placement atop the other sclerites results from a backwards slippage. The sclerite derives from one of the anterior segments, as indicated by the position on top of the rest, an angle of the longitudinal fold around 140°, and a higher density of rugae than have the following sclerites.

Remarks. Sclerites with a displaced umbo have previously only been reported from plumulitids, see e.g. Barrande (1872); and Etheridge (1878; although he first considered it to be a turrilepadid); and Jell (1979), where such an umbo is restricted to outer anterior sclerites. Inner sclerites with a displaced umbo, however, are previously unknown.

Reconstruction. The three illustrated specimens (LO 7371t, LO 7379t and PMU G1020) and comparisons with other turrilepadids and plumulitids give a relatively clear picture of the appearance of the scleritome.

Turrilepas sp. A has a scleritome consisting of at least 25 segments and a distinct anterior end as in *T. wrightiana* (Adrain *et al.* 1991). According to Adrain *et al.* (1991), the anterior end in *T. wrightiana* lacks outer sclerites on the two first segments. The inner sclerites of these two segments differ in some ways: they have a higher density of rugae than subsequent inner ones, and they exhibit a larger angle of the longitudinal fold. Not until segments 5–6 does the angle of the longitudinal fold achieve its stable value of 90°. The outer sclerites of *T. wrightiana* are of uniform appearance, however, throughout the scleritome. In plumulitids the anterior structure is similar, but there are species with modified outer sclerites at the anterior end. This is the case for e.g., *P. richorum*, which lacks outer sclerites of the first two segments, whereas outer sclerites of the three subsequent segments have modified apical regions (see Jell 1979 for a detailed description). In *Turrilepas* sp. A the anterior structure is suggested to be as follows. Segments 1–2 consist only of inner sclerites, flatter, and with a relatively high density of rugae. Specimen LO 7371t (Pl. 1, figs 1–6) and PMU G1020 (Pl. 1, fig. 8) have inner sclerites with a higher density of rugae (their angle of the longitudinal fold is larger than 90°, indicating an anterior position). Judging primarily from their size, they do not seem to derive from the very first segment. They are more probably sclerites representing a transition towards the general form of inner sclerites. LO 7371t seems to have lost the outer sclerites of the first segments exposed in the specimen. Segment 3 in *Turrilepas* sp. A presumably had modified outer sclerites (Pl. 1, fig. 8). Due to the fact that only one certain modified sclerite has been recovered, it is not clear in how many segments they were present. They were most probably restricted to the anterior region, as indicated by other species with modified outer sclerites, where they characterize the anterior end of the scleritome. In the turrilepadids this anterior end continues only to segment 5 or 6. Thus the unmodified outer sclerites in *Turrilepas* sp. A appear no earlier than segment 4 and presumably no later than segment 6. By then the inner sclerites have attained the appearance of subsequent ones, and the angle of the longitudinal fold reached the general value of 90° also by segment 6. The largest part of a turrilepadid scleritome is of a uniform arrangement, with a virtually square body cross section resulting from the 90° angle of the longitudinal fold (see especially *T. modzalevskae* in Adrain *et al.* 1991, pl. 2, figs 4–5). The situation in *Turrilepas* sp. A is consistent with this arrangement. The mid-part of the scleriitome in *Turrilepas* sp. A involves at least *c.* 18–20 segments. The posterior end is unknown in *Turrilepas* sp. A as in other turrilepadids. A general decrease in segment size may be the only modification.

Functional morphology. The articulation of the turrilepadid scleritome differs from that of lepidocoleids; turrilepadids were not able to close their scleritome. This is contrary to the opinion of Jell (1979), who considered turrilepadids to be able to close their scleritome fully, like lepidocoleids. Adrain (1992) concluded that it was not very likely that turrilepadids could ever close the scleritome entirely because of the medial overlap and posterior imbrication of sclerites. However, the amount of movement possible in the transverse plane was presumably very small and most likely had very little to do with attempts to close the scleritome. The strong overlap and imbrication of both inner and outer sclerites would prevent all larger movements of the sclerites in that direction. The rugae on all sclerites are asymmetrical, with a form reminiscent of terrace sculptures in burrowing invertebrates (e.g. Savazzi 1994). The steeper sides of the rugae face approximately posteriorly. The distinct pattern of rugae in *Turrilepas* sp. A may be explained partly by the need for reinforcement in areas that otherwise may have constituted weak points. A possible function of the outer sclerites could have been to soften the sediment, either in search for food or perhaps in the process of burrowing, or both. It may possibly be argued that the outer sclerites were used to close the scleritome, at least partly, but considering the arrangement of the scleritome with the overlap and imbrication of sclerites, other functions seem more probable. Besides burrowing for protection, the possibility of enrolling sideways in a manner similar to millepedes should also be considered.

The growth of machaeridian scleritomes holds part of the key to understanding the biology and phylogeny of the group. Adrain *et al.* (1991) suggested that an organism with a fixed number of sclerites grew at the same rate with rugae deposited in an incremental manner. As stated by these authors, this is incompatible with serial addition of segments. Based on the collections in The Natural History Museum (London), this seems to be a plausible hypothesis. Some specimens, however, have sclerites with an aberrant growth pattern which does not conform to incremental growth and such sclerites need to be explained. One such sclerite is figured on Plate 1, figures 5–6; this inner sclerite gives the impression of having been incorporated at a later stage and having achieved its size quite rapidly. A general disturbance of growth should have been traceable on all sclerites at the same intervals. Perhaps this reflects later incorporation of this specific sclerite, but it is not clear whether severe damage led to the replacement of the injured sclerite with a new one or whether it indicates some other aspect of machaeridian growth.

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ANETTE E. S. HÖGSTRÖM

Institute of Earth Sciences
Department of Historical Geology and Palaeontology
University of Uppsala
Norbyvägen 22
S-752 36 Uppsala, Sweden
e-mail Anette.Hogstrom@pal.uu.se

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